The status of the South African galaxiid (Pisces, Galaxiidae)

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ABSTRACT

Study of general morphology and osteology shows that the South African galaxiid belongs in the genus *Galaxias*. *Agalaxis* Scott is a synonym of *Galaxias*. Data also support earlier opinions that there is only one variable species of *Galaxias* in South Africa—*G. zebratus* (Castelnau)—which is described and figured.

INTRODUCTION

Four species of *Galaxias* have been described from South Africa, viz., *G. zebratus* (Castelnau), *G. punctifer* (Castelnau), *G. capensis* Steindachner and *G. dubius* Gilchrist and Thompson. Castelnau (1861), in error, described *G. zebratus* and *G. punctifer* in *Cobitis* (Ostariophysi, Cobitidae—the loaches), and Steindachner (1894—*G. capensis*) first placed the South African form in *Galaxias*. Boulenger (1905) and Regan (1905) both recognized that Castelnau's two species belonged in *Galaxias*, Regan also showing that *G. capensis* Steindachner is a junior synonym of *G. zebratus* (Castelnau). Gilchrist and Thompson (1917) described a fourth species, *G. dubius*, but remarked that "It is not improbable that the three species described [*G. zebratus*, *G. punctifer* and *G. dubius*] may on examination of more extensive collections prove to be merely varieties of one species". This proved to be true. Barnard (1943) studied extensive collections (4 700 specimens) from diverse localities throughout the range of the genus *Galaxias* in South Africa, and reached the conclusion that there is only one variable species. The two names published by Castelnau (1861) had equal taxonomic status before Barnard's revision, but as a result of Barnard's choice of *G. zebratus*, this name becomes the senior synonym (Barnard, 1943, first reviser; International Code of Zoological Nomenclature 1964, Article 24 (a) (1)).

Barnard's view has become generally accepted, although some workers have listed two (Scott, 1936, 1966) or even four species (Whitley, 1956). However, those workers familiar with the South African galaxiid seem satisfied that there is but a single species of galaxiid in South Africa, e.g., Harrison, 1960, 1967; Jubb, 1965, 1967; Stokell, 1950, 1953. Nothing in the present study suggests that this is open to serious question.

Despite this earlier work of Barnard's, a full description of the species has not been prepared—all that exists is a four-line diagnosis followed by an extensive but general discussion of variability in several characters. Barnard's diagnosis has been repeated by Jubb (1965, 1967). One of the objectives of this paper is to publish a full description of the South African galaxiid, to facilitate its comparison with other galaxiids. The description conforms to those already published for New Caledonian, New Zealand and South American galaxiids (McDowall, 1968a, 1970a, 1971).

A fifth galaxiid name appears in the literature (Weber, 1895) which quite obviously refers to South African galaxiids, viz., *G. africanus*. This name occurs in a brief communication, which is quoted here because of its obscurity:

> De Heer Weber deelt mede, dat de door hem op de Vergadering van 30 Maart 1895 beschrevene n. sp. *Galaxias africanus* kort de voren door Steindachner als *Galaxias capensis* in de wetenschap was ingevoerd. De door hem gegeven naam moet dus vervallen.

In brief, it is pointed out that *Galaxias africanus* described by Weber at a meeting on 30 March 1895, is the same as *G. capensis* Steindachner. The note states that the name *G. africanus* must therefore be dropped.

As far as I can determine, the name *G. africanus* does not appear previously in the literature, and there does not seem to be a published description. *Galaxias africanus* is thus a *nomen nudum*.

A more serious concern of the present paper is the generic status of the South African galaxiid. Apart from the obvious erroneous inclusion of the species in *Cobitis* by Castelnau (1861), the following genera have been used for *G. zebratus:*

Galaxias Cuvier: Regan, 1905; Barnard, 1943; Jubb 1965, 1967; McDowall, 1969; and others.
Galaxias subgenus *Agalaxis* Scott: Scott, 1936.
Paragalaxias Scott: Stokell, 1950.
Agalaxis Scott: Scott, 1966.

That *G. zebratus* is a galaxiid is clear; its lack of scales, dentition, fin positions, distribution of head pores, number of pelvic and caudal fin rays, and the general osteology of *G. zebratus* all conform closely in most details with other galaxiids (McDowall, 1969).

Scott (1936) suggested that *G. zebratus* should be placed in a new subgenus *Agalaxis* within *Galaxias* because of its six rayed pelvic fins. Barnard (1943), on account of variation in the number of pelvic fin rays demonstrated by Stokell (1940), concluded that Scott's subgeneric division could not be sustained, although he also pointed out that the low vertebral number in *G. zebratus* "40 (occasionally 39 or 41) . . . might be considered to justify generic rank" (Barnard, 1943, 231—2). In spite of this, Barnard retained *G. zebratus* within *Galaxias*. Stokell (1945) rejected the subgenus *Agalaxis* on the same grounds as Barnard, viz., intraspecific variation in pelvic fin ray counts. However, Stokell later (1950) re-examined *G. zebratus*. He then decided that it belongs in the genus *Paragalaxias* Scott, but did not indicate the diagnostic characters that prompted this decision. He noted that, "The genus *Paragalaxias* is now much less distinct than it appeared when first described [Stokell, 1945, excluded *Paragalaxias* from the Galaxiidae but reinstated it in 1950] and it seems possible that it may ultimately intergrade with *Galaxias*, but in the present state of knowledge, the species *dissimilis* and *zebratus* form a natural group which requires to be distinguished in some way. The provisional retention of the genus *Paragalaxias* appears to be the course least likely to cause further complications" (Stokell, 1950:3). Low vertebral number and a short predorsal dimension seem to be the characters which Stokell used to distinguish *Paragalaxias* from *Galaxias*.

Scott (1966) further dealt with the galaxiid genera. He restored *G. zebratus* to *Agalaxis*, and elevated *Agalaxis* from subgeneric to generic rank, following the tentative suggestion of Barnard (1943). He distinguished *Agalaxis* from *Galaxias*, *Saxilaga* Scott and *Neochanna* Günther by its low vertebral number, from *Lepidogalaxias* Mees (not a galaxiid—McDowall, 1969) by absence of scales and other differences, from *Brachygalaxias* Eigenmann by the position of the dorsal origin and the absence of a pelvic-anal keel, and from *Paragalaxias* by the relative positions of the dorsal and anal fins, the size of the dorsal fin, and the disposition and number of cephalic lateral line pores. Scott (1966) discarded pelvic fin ray number (Scott, 1936) as a generic character for *Agalaxis*.

In a recent paper (McDowall, 1969), in which the broad relationships of the galaxioid fishes were examined, I included *G. zebratus* in *Galaxias*, making brief comments on its osteology, but did not consider in detail the generic taxonomy of Scott (1966). This consideration follows here.

MATERIAL AND METHODS

The methods of study adopted here are the same as I have used in previous galaxiid studies (McDowall, 1970a, 1971) and in general, follow Hubbs and Lagler (1958). Vertebral counts, taken from both alizarin preparations and radiographs, exclude hypural centra. Fin ray counts include all segmented rays, except in the caudal, where a standard principal ray count is given. Gill raker counts are difficult as the dorsal and ventral rakers are very small and often embedded in mucus. Thus the counts are not especially accurate and those taken from alizarin preparations tend to be higher than those taken from formalin or alcohol preserved specimens.

Material studied comprised four small samples generously provided by Mr R. A. Jubb, Albany Museum, Grahamstown (AMG), South Africa. These samples came from the following localities: Olifants River system (AMG PF 1356); Eerste River system (AMG no catalogue number); Witels River, near George (AMG PF 217); a small stream east of George (AMG no catalogue number). These samples encompass the extremes of the range of *G. zebratus* in South Africa, from the north-west (Olifants) to the south-east (George).

GENERIC POSITION OF THE SOUTH AFRICAN GALAXIID

A comprehensive description of *G. zebratus* is given below and data discussed are, in part, presented in this description and Tables 1 and 2. The tidiest way of considering the problem of *G. zebratus* and the status of *Agalaxis* would seem to be to consider each of the purported diagnostic characters of *Agalaxis* in turn, in relation both to the principal galaxiid genus *Galaxias*, and to the other derived genera.

Of the diagnostic characters listed by Scott for *Agalaxis* (Scott, 1966) some are diagnostic of the family (McDowall, 1969) (reworded from Scott, 1966): scales absent; teeth in jaws and on mesopterygoids (entopterygoids) uniserial, conical, lingual teeth biserial, decumbent teeth associated with all tooth rows. Other characters come within the range of variation of genus *Galaxias*, viz., anal base longer than or equal to length of dorsal base, the number of dorsal fin rays equal or subequal to the number of anal rays, dorsal fin largely over anal fin; pelvic fin rays modally six (usually seven in *Galaxias*, but sometimes six, e.g. *G. divergens* Stokell); branchiostegals six or seven; gill rakers 2—3 and 9—10; size small. Characters remaining from Scott's diagnosis which may be regarded as diagnostic for *Agalaxis* are number of vertebrae (38—41); number of branched caudal rays (modally 12); position of dorsal fin (0,59—0,67 of standard length); disposition of cephalic lateral line pores; size at sexual maturity (about 40 mm (T.L. ?)).

Number of vertebrae: Scott (1966) placed great emphasis on vertebral number in the Galaxiidae, suggesting subdivision of the family into two groups, one including forms with more than 50 vertebrae and the other those with less than 50 vertebrae. But some species, e.g., *G. divergens* Stokell (47—53 vertebrae), *G. prognathus* Stokell (50—56). *G. gracilis* McDowall (47—53) (McDowall, 1970a, 1972), have vertebral counts spanning the point of division, but are closely related to other species which fall entirely within one of such subfamilial divisions and use of vertebral number in the classification of the Galaxiidae has little value.

G. zebratus has 36 to 42 vertebrae (Table 1). *Nesogalaxias neocaledonicus* (Weber and de Beaufort) has 41—43 (McDowall, 1968a); *Brachygalaxias bullocki* (Regan) has 38—42 (McDowall 1971); *Paragalaxias shannonensis* (Scott) (redescribed as *P. dissimilis* (Regan) by Stokell, 1950, a synonymy rejected by Scott (1966) who I tentatively follow) has 37—43 vertebrae (Stokell, 1950). Thus *G. zebratus* differs from all other *Galaxias* in having fewer vertebrae, but has about the same number as each species in the monotypic genera *Nesogalaxias* Whitley, *Brachygalaxias* Eigenmann and *Paragalaxias* Scott.

Number of caudal fin rays: Scott gave the branched caudal fin ray count as "modally 12". The number of principal rays is modally 14 with a range of 13 to 15 (Table 1). A usual count for *Galaxias* is 16, but *G. divergens* has a modal count of 15 (range 14—16); *Neochanna burrowsius* (Phillipps) has 13 (range 11—14) and *N. apoda* Günther has a modal count of 16 but a wide range (13—17). *Brachygalaxias bullocki* has 15 rays (range 14—16). Thus the low caudal fin ray count in *Galaxias zebratus* overlaps counts in other *Galaxias*, *Brachygalaxias* and some *Neochanna*.

Position of dorsal fin insertion: Scott (1966) gave the dorsal fin insertion of *G. zebratus* as 0,59—0,67 of standard length (i.e. 59—67%). My measurements gave figures of 59,3 to 67,0% (Table 2). Many *Galaxias* have this dimension 70% or more of standard length, a few New Zealand species have it 65—70% (McDowall, 1970a) these being species in which

Table 1. Meristic variation in *Galaxias zebratus*

Dorsal fin rays	9	10	11					*Mean*
Oliphants R.	1	4	4					10,33
Eerste R.	1	7	2					10,10
Witels R.	4	3	3					9,90
"George"		5	5					10,50
Anal fin rays	9	10	11	12	13			
Oliphants R.		2	3	4				11,22
Eerste R.	1	2	7					10,60
Witels R.		2	3	4	1			11,40
"George"			3	6	1			11,80
Pectoral fin rays	14	15	16	17				
Oliphants R.	3	1	4	1				15,33
Eerste R.	1	5	3	1				15,40
Witels R.	7	3						14,30
"George"	3	5	2					14,90
Vertebrae	36	37	38	39	40	41	42	
Oliphants R.	1	1	7					37,66
Eerste R.		1	5	6				38,42
Witels R.					1	6	4	41,27
"George"					3	7	4	41,07
Caudal fin rays	13	14	15					
All samples	2	36	1					13,99
Pelvic fin rays	6	7						
All samples	35	4						6,10
Branchiostegals	5	6	7					
All samples	3	24	12					6,23
Gill rakers	8	9	10	11	12			
All samples	8	10	13	7	1			9,56

TABLE 2: Variation in body proportions in *Galaxias zebratus* (figures given as percentages of denominator in ratio).

	Oliphants R.			Eerste R.			Witels R.			"George"		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
Total length/standard length	84,9	86,52	88,7	84,9	86,03	87,1	84,8	86,55	88,9	84,6	86,43	87,9
Body depth at vent/standard length	12,7	14,54	16,4	14,0	15,40	17,0	10,5	12,97	13,8	11,9	12,87	13,8
Length of caudal peduncle/standard length	17,8	20,11	23,1	17,9	19,93	22,0	18,9	20,54	21,6	18,7	20,21	21,7
Length of caudal peduncle/depth of peduncle	42,4	50,73	60,0	46,2	53,91	61,8	39,0	46,51	54,1	41,0	45,60	50,0
Predorsal length/standard length	60,3	63,46	66,4	59,3	60,96	62,5	61,6	63,85	66,8	62,5	64,66	67,0
Predorsal length/preanal length	94,0	95,81	98,9	91,7	93,66	96,0	94,2	97,43	100,0	95,5	97,41	100,0
Length of dorsal fin base/standard length	11,9	13,69	15,1	13,0	14,79	16,1	11,1	12,34	13,9	11,4	11,89	12,7
Length of dorsal fin base/maximum length of fin	61,5	70,19	79,3	65,5	72,00	82,6	53,5	65,01	73,5	56,8	64,24	67,9
Length of anal fin base/standard length	12,7	13,77	15,1	14,3	15,30	15,9	13,5	14,65	16,1	13,1	14,41	15,8
Length of anal fin base/maximum length of fin	64,0	69,27	73,3	69,2	74,20	79,3	67,5	73,73	82,8	61,9	70,09	81,1
Prepelvic length/standard length	49,3	51,31	54,1	48,2	49,50	50,9	47,7	49,83	51,7	48,8	50,24	53,5
Pectoral pelvic length/standard length	24,0	25,69	28,1	24,1	26,35	29,1	25,5	28,24	30,6	25,0	26,57	28,3
Pelvic-anal length/standard length	14,4	15,47	18,0	14,4	17,21	19,6	17,0	18,55	20,6	15,7	18,00	19,3
Pectoral fin length/pectoral-pelvic length	46,3	49,09	50,0	46,9	53,69	60,0	37,9	45,21	48,9	46,5	51,57	56,8
Pelvic fin length/pelvic-anal length	56,0	65,64	81,3	53,6	63,28	76,5	41,0	53,51	60,9	47,2	54,91	65,7
Head length/standard length	23,7	25,61	27,4	23,7	25,50	26,7	22,4	24,32	26,1	23,2	24,61	26,0
Head width/head length	45,2	48,91	55,6	46,6	54,36	58,7	47,3	51,65	54,8	44,0	49,13	52,4
Head depth/head length	50,0	55,01	61,1	55,3	59,29	65,6	48,9	53,35	58,1	40,0	46,01	52,2
Snout length/head length	22,6	25,10	29,3	22,7	25,98	29,8	24,0	27,29	34,1	23,4	25,91	30,0
Postorbital head length/head length	51,4	54,24	58,3	47,7	53,26	60,8	50,0	52,56	55,8	51,1	52,37	54,5
Interorbital width/head length	25,0	32,20	36,1	28,6	33,83	39,3	27,7	31,27	34,6	25,0	28,38	32,5
Diameter of eye/head length	23,8	26,06	28,6	18,2	22,70	25,0	19,0	21,23	23,8	18,0	22,03	23,9
Length of upper jaw/head length	30,9	32,84	34,3	31,5	34,01	36,8	25,5	30,32	33,3	29,3	32,55	37,0
Length of mandible/head length	28,6	30,90	34,2	27,3	31,25	34,5	25,5	27,85	31,8	28,0	30,18	34,8
Width of gape/head length	25,7	27,74	31,7	27,3	31,00	38,0	25,5	27,74	29,5	23,8	27,30	30,5

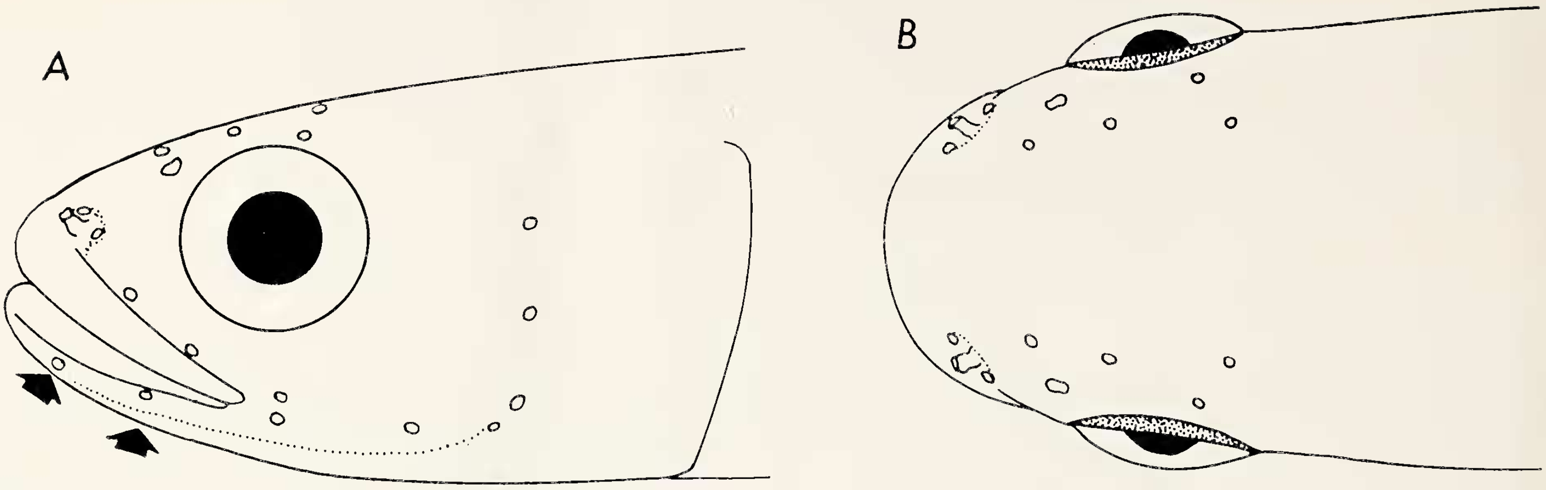

Fig. 1. Disposition of laterosensory pores on head of a generalized galaxiid. A. Lateral head; B. dorsal head. Arrows indicate pores lacking in *Galaxias zebratus*.

the caudal peduncle is especially long; thus, when the caudal peduncle is particularly long, the dorsal fin is further forward in the standard length. This is true, for instance, in *G. paucispondylus* Stokell (McDowall, 1970a)—predorsal length/standard length is 65,8—72,5% and length of caudal peduncle/standard length 16,8—21,4%. *G. zebratus* also has a particularly long caudal peduncle—length of caudal peduncle/standard length is 17,8—23,1%. The apparently forward position of the dorsal fin origin in both these species is a direct consequence of the long caudal peduncle, and if any character should be regarded as distinctive for *G. zebratus* it is therefore the length of the caudal peduncle. However, the peduncle is not so long or so different from other galaxiids as to justify use as a generic character.

Disposition of cephalic lateral line pores: The positions of lateral line pores on the head of *Galaxias* are fairly constant (Fig. 1). Although occasionally a fish may differ from this pore pattern, there is considerable intra- and inter-specific stability. The South African species lacks the two pores present beneath the lower jaw in *Galaxias* (those indicated by an arrow in Fig. 1). Curiously, *Brachygalaxias bullocki* lacks these same two pores (McDowall, 1971). Thus, *G. zebratus* differs from all galaxiids for which pore patterns have been described, except *B. bullocki*, in its laterosensory pore patterns.

Sexual maturity: Scott (1966) noted that *G. zebratus* may be sexually mature at 40 mm (T.L.?). Little is known of size at maturity in galaxiids, but *G. maculatus* may mature at 54 mm L.C.F. (McDowall, 1968b), *G. divergens* Stokell at 50 mm L.C.F. (Hopkins, 1971), *G. gracilis* McDowall at as little as 30 mm, although more usually at 50 mm or more (McDowall, 1972). *Nesogalaxias neocaledonicus* grows to 76 mm but is rarely more than 50 mm and most adults and sub-adults in collections I have examined have been between 40 and 50 mm (McDowall, 1968a). *Brachygalaxias bullocki* reaches 60 mm, but rarely exceeds 50 mm (McDowall, 1971), so probably matures at 40—50 mm.

It is possibly true that *G. zebratus* reaches maturity at a smaller size than many galaxiids, but the difference, if any, is slight, and this character is of no consequence to the generic taxonomy of galaxiids.

Osteology: Neither Scott (1936, 1966), nor others, have discussed osteology in relation to the generic classification of *G. zebratus*. Previously (McDowall, 1969:805) I noted that "the supracleithra are somewhat expanded to form triangular plates; the palatine spur is lacking, and in fishes examined there was no ethmoid ossification". In fact it is the post-temporal, not the supracleithrum which is expanded. Study of further specimens otherwise confirmed these characteristics.

Variability in the caudal skeleton noted for other galaxiids (McDowall, 1969) in the occurrence and form of neural and haemal arches and spines is exemplified in *G. zebratus*, e.g., in two specimens cleared and stained one had one full neural arch and spine, one somewhat reduced arch and spine, and one full haemal arch and spine on the urostylar vertebra, in addition to the normal parhypural and five hypurals. The other specimen had only one neural arch and spine and no haemal arch and spine on the urostylar vertebra. Clearly there is variable fusion of terminal vertebrae in *Galaxias zebratus* and other galaxiids.

Fusion of hypural elements is evident. In one specimen, the parhypural and hypurals one and two are fused, hypural three is free, and hypurals four and five are fused. In the other, hypural three is proximally fused to but distally free from hypurals four and five. Study of further material showed that hypurals four and five are not always completely joined. Similar fusion is evident in *Brachygalaxias bullocki* (Greenwood *et al.* 1966, fig. 4; McDowall, 1969). There is nothing unique in the osteology of *Galaxias zebratus* that is of sufficient significance to justify generic separation of this species.

Reviewing this discussion, *G. zebratus* differs from all *Galaxias* chiefly in its low vertebral number and the absence of two laterosensory pores beneath the lower jaw on each side. It also has a long caudal peduncle. It differs from MOST *Galaxias* in its reduced number of caudal fin rays, although there is overlap. It clearly does not have affinities with the *Neochanna-Saxilaga* group of Tasmanian—New Zealand mudfishes with their adaptations to swamp dwelling and aestivation during drought. *Paragalaxias* is ill-defined and requires study, but it seems to be based on the fact that the dorsal fin is above the pelvic fins (above anal in *Galaxias* and *G. zebratus*) and that the dorsal fin has more rays than the anal (subequal in *Galaxias* and *G. zebratus*). There is no evidence of relationship between *G. zebratus* and *Nesogalaxias*, the status of which depends on the latter's unique loss of pleural ribs. Although *G. zebratus* is similar to *Brachygalaxias* in its low vertebral count, its loss of laterosensory pores beneath the lower jaw, and its small size at maturity, it does not possess the characters that quite clearly distinguish *Brachygalaxias* from all other galaxiids, i.e., two distinct ural centra and an elongate alveolar process on the premaxilla which entirely excludes the maxilla from the gape (McDowall, 1969, 1971). These differences exclude *G. zebratus* from *Brachygalaxias*. Thus *G. zebratus* may be considered to be excluded from all the other minor galaxiid genera that have been formally described (*Lyragalaxias* Whitley and *Querigalaxias* Whitley await formal description, although they do have taxonomic status, having been applied to stated galaxiid species). The question for which an answer is now required is thus whether *G. zebratus* belongs in *Galaxias*, or in a separate genus, which would be *Agalaxis* Scott, 1936.

It is important and appropriate, at this point, to discuss the circumstances surrounding the evolution of life history patterns in the Galaxiidae, and the morphological changes which have accompanied such life history changes.

From osteological study it appears to me that the most primitive, unspecialized galaxiids are the diadromous species that have larvae which spend the winter in the sea (McDowall, 1969). In these species, spawning is in autumn, the eggs are relatively small and numerous, the larvae go to sea, probably soon after hatching, and they return from the sea as very characteristic, elongate, slender, transparent juveniles. Such a pattern is known in *G. maculatus* (Jenyns) (Australia, New Zealand, South America), *G. truttaceus* Valenciennes (Australia), *G. brevipinnis* Günther (Tasmania, New Zealand), *G. fasciatus* (Gray), *G. postvectis* Clarke and *G. argenteus* (Gmelin) (all New Zealand) and is suspected in *G. platei* Steindachner (South America) (McDowall, 1970a, b, 1971). Many of these species have lacustrine populations in which the life history pattern is structurally similar, the lake replacing the sea. Lake populations are similar to diadromous ones, in most characters, except that vertebral number may be reduced in the lake fishes. The diadromous life history pattern appears to be primitive for the family Galaxiidae, and this view is supported by the widespread occurrence of diadromy of various types throughout the galaxioid fishes (sub-order Galaxioidei, families Galaxiidae, Aplochitonidae, Retropinnidae and Prototroctidae—McDowall, 1969). Apart from *Gallaxias*, all the galaxiid genera consist wholly of non-diadromous and completely fresh water species. The fact that they are placed in different genera (mostly monotypic genera) points to specialization, and the fact that they are all confined to fresh water and have dispensed with migration suggests, to me, that their specializations are connected with their adoption of a purely freshwater life. Scott (1966) listed morphological peculiarities of *Brachygalaxias*, *Paragalaxias* and *Agalaxis* in which they depart from *Galaxias*—small size, reduction in the number of vertebrae, number of ova, number of pelvic fin rays, number of cephalic lateral line pores with some instability, movement of the dorsal, anal, and pelvic fins along the trunk, large eye. All of these are changes that occur within diadromous and non-diadromous species of *Galaxias*. These changes in *G. zebratus* can therefore be identified as those which may occur in *Galaxias* when a species discards the migratory and marine phases of its life history.

This is seen in *G. zebratus;* and its morphological peculiarities—limited to reduced number of vertebrae, loss of two cephalic laterosensory pores, elongate caudal peduncle, fusion of hypurals in the caudal skeleton, etc.—do not seem to justify generic recognition. Although *G. zebratus* has diverged from the primitive galaxiid pattern in a few characters, it is a "very ordinary" freshwater limited galaxiid. From consideration of both general morphology and osteology there seems little reason for retaining the genus *Agalaxis* Scott which is therefore placed in synonymy of *Galaxias* Cuvier.

GALAXIAS CUVIER

A full diagnosis of *Galaxias* was published by McDowall (1970a), and the reader is referred to that account. Inclusion of *G. zebratus* in *Galaxias* does not require modification of this generic diagnosis.

Galaxias zebratus (Castelnau), 1872

Cobitis zebratus Castelnau, 1861: 56 (holotype: unknown; reported lost by Jubb, 1965: 16; locality: Cape Town, South Africa).

Cobitis punctifer Castelnau, 1861: 56 (holotype: unknown; also reported lost by Jubb, 1965: 16; locality: Cape Town, South Africa).

Galaxias capensis Steindachner, 1894: 460 (syntypes (3): Naturhistoriches Museum, Vienna No. 6—466, not seen); locality: Lourens River, south-west Cape; Weber, 1895; XXXIX; Gill, 1896: 366; Weber, 1897: 154; Whitley, 1956: 34.

Galaxias zebratus: Regan, 1905: 367; Boulenger, 1905: 51; Waite, 1909: 586; Boulenger, 1915: 12; Gilchrist and Thompson, 1917: 471; Barnard, 1943: 236; Harrison, 1952: 50; 1953: 128; Whitley, 1956: 34; Harrison, 1960: 14; Jubb, 1963: 8; 1964: 18; 1965: 15; Harrison, 1966: 23; 1967: 29; Jubb, 1967: 77; Breder and Rosen, 1966: 132; Anon. 1968a: 47; 1968b: 100; McDowall, 1969: 810.

Galaxias punctifer: Regan, 1905: 367; Boulenger, 1905: 51; Waite, 1909: 586; Boulenger, 1915: 12; Gilchrist and Thompson, 1917: 472; Barnard, 1943: 231; Whitley, 1956: 34; Jubb, 1963: 8; 1964: 18; Breder and Rosen, 1966: 132.

Galaxias dubius Gilchrist and Thompson, 1917: 472 (holotype: unknown; paratypes (3); Museum National d'Histoire Naturelle, Paris, France 23.35, not seen; locality: George River, Cape Province, South Africa); Whitley, 1956: 34.

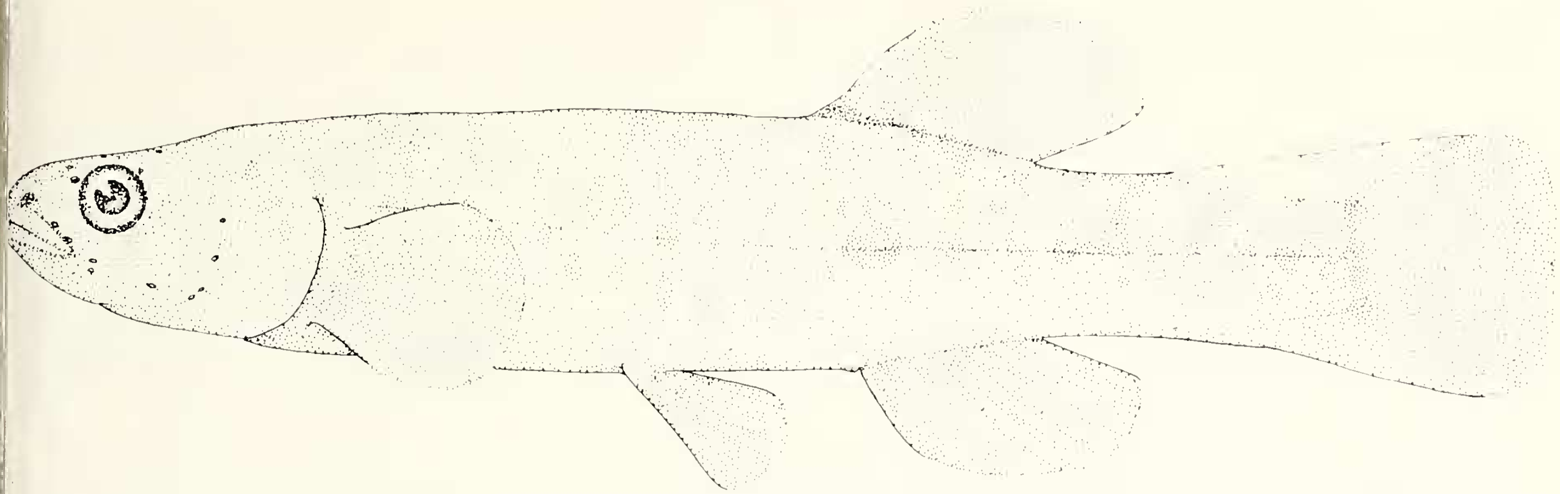

Fig. 2. *Galaxias zebratus* (Castelnau), 50½ mm L.C.F., Eerste R., Cape Province, South Africa.

Galaxias (*Agalaxis*) *zebratus:* Scott, 1936: 105.
Galaxias (*Agalaxis*) *punctifer:* Scott, 1936: 105.
Paragalaxias zebratus: Stokell, 1950: 3; 1953: 49.
Agalaxis zebratus: Scott, 1966: 253.
Agalaxis punctifer: Scott, 1966: 253.

Description: Trunk cylindrical, moderately stout, laterally compressed on caudal peduncle, which is very long; dorsal and ventral trunk profiles about parallel; lateral line a definite mid-lateral crease. Head obtuse, of moderate size, about as broad as deep, snout rather blunt, rounded. Eye of moderate size, set high and well forward in head, interorbital more or less flat. Mouth terminal, jaws equal, cleft slightly oblique reaching to, or a little beyond anterior eye margin. Jaws without canines; mesopterygoidal teeth moderately well developed; anterior, tubular nostril strongly developed and projecting horizontally forward almost to tip of snout; pyloric caeca lacking; gill rakers short.

Fins slightly fleshy at bases and small. Dorsal fin origin well forward in standard length (due largely to great length of caudal peduncle), anal fin originates below or a little behind dorsal fin origin. Both fins short based, middle rays longest, with distal margins rounded. Pelvic fins inserted at about midpoint of standard length, pelvic-anal interval quite short, fins small. Pectoral fins short and fan-shaped, middle rays a little longer than marginal ones, fin inserted moderately high behind opercular apertures. Caudal fin long, generally truncated, sometimes slightly emarginate or rounded; peduncle flanges low but extending well along peduncle towards bases of dorsal and anal fins.

Variation: Meristic and morphometric data from the four populations studied are given in Tables 1 and 2. These data show *G. zebratus* to be a rather variable species in a few characters, e.g., vertebral number (Table 1), but none of the populations is strikingly different from the others, and the variation seems to represent mosaic evolution in a series of allopatric populations. The south-eastern populations (Witels and George) have fewer vertebrae than the western (Eerste) and northern (Olifants) populations, but the variation is no greater than is evident in comparable, widespread freshwater limited species like *G. divergens* Stokell and *Brachygalaxias bullocki* (Regan) (McDowall, 1970a, 1971). Consideration of the data in Tables 1 and 2 does not suggest that more than one species is present. Thus, Barnard's (1943) analysis of a few characters in a great number of samples, and my analysis of many characters in a few small samples reach the same conclusion.

Colouration: Highly variable, according to the nature of the habitat, varying from heavily barred to almost colourless, with all intermediates (see Barnard, 1943). Fishes I have seen usually have had somewhat regular rows of darker blotches across the back and extending down each side to varying degrees. Some have no more pigment than a general covering of tiny melanophores.

SIZE: *G. zebratus* is reported by both Barnard (1943) and Jubb (1967) to reach a length of 75 mm.

HABITAT AND LIFE HISTORY: Little is recorded of either habitats or life history of *G. zebratus*. Literature sources show that it occurs in both clear and brown-stained waters, and in streams and lakes, which may be either acid (pH 5—6,5) or alkaline (pH 8—9) (Barnard, 1943; Jubb, 1967). Barnard found *G. zebratus* mostly in small streams, not the main rivers, on either muddy or gravelly substrates. *G. zebratus* clearly occurs in diverse conditions in lakes and streams.

Barnard (1943) summarized knowledge of the life history of *G. zebratus*, and little new information has since been published. Barnard's information is summarized briefly here. Maturity is reached at a small size, about 40 mm, the ripe eggs are moderately large, demersal, and number 30—40, rarely 50 or more. Spawning, and the entire life history are freshwater, although brackish water may be tolerated. Breeding is suspected to occur throughout much of the year. *G. zebratus* thus has a life history similar in essential details to freshwater limited galaxiids from other areas (McDowall, 1969, 1970a, 1971).

Jubb (1967) reported that *G. zebratus* is "omnivorous . . . feeding primarily on small aquatic animals".

Distribution, zoogeography and relationships: Jubb (1967) summarized the range of *G. zebratus* as the "south coastal drainage basin from the Olifants River system eastwards to the Kaimans River east of George". From Barnard's (1943: 123—4) list of geographical localities, his map, (p. 233), and from subsequent reports by other workers (Anon. 1968a, b; Harrison, 1960, 1966, 1967) it is clear that *G. zebratus* is widespread and generally distributed in lakes and streams between the two river systems named by Jubb. It tends to be coastal and lowland, although it penetrates far inland in some rivers, e.g., tributaries of the Olifants and Gouritz rivers.

Zoographically, *G. zebratus* is something of a novelty in the African freshwater fish fauna, as it is one of very few members of that group of fishes not derived from the fauna of the great tropical African rivers, and the only species of southern-temperate relationships. Galaxiids are temperate and cold-temperate fishes so that the restriction of *G. zebratus* to the far southern tip of South Africa is not surprising. However, it could perhaps have been expected to occur in the mountains. In view of the known salt tolerances of a good many galaxiids (see McDowall, 1964, 1970a) it seems reasonable to propose that *Galaxias* reached Africa across oceanic gaps, presumably from South America, since this is both the nearest land mass with *Galaxias* present, and is in a favourable direction if oceanic currents were instrumental in bringing *Galaxias* to the African continent. It is therefore, perhaps, of interest that *G. zebratus* shares with *Brachygalaxias bullocki* in Chile, the loss of laterosensory pores beneath the lower jaw. The disposition of these pores is a conservative character throughout the Galaxiidae, varying little within or between species. The similar divergence from the usual pattern in both *G. zebratus* and *B. bullocki*, may therefore be an indication of phylogenetic relationship. However, the possibility of convergence is sufficiently real to preclude any further speculation on the relationships of *G. zebratus*.

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